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Are spruce boles hot spots for enchytraeids in clear-cut areas?

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I investigated the effects of stem wood on enchytraeid abundance and size distribution in a Norway spruce forest after clear-cutting. Eighteen plots (16 m^2) were prepared and planted with Norway spruce according to normal forestry practice and pieces of logs discarded by the logging machine were returned to nine plots. Six years after the clear-cutting enchytraeid abundance was significantly lower at 10 cm distance from added spruce boles than next to the boles and than in the control plots. Enchytraeids were significantly smaller in control plots than in wood plots and in an adjacent forest. Wood addition significantly decreased the biomass of ground vegetation six years after the clear-cutting, possibly because wood-decomposing fungi immobilized soil nutrients. Because enchytraeids feed on both fungal hyphae and plant litter, the beneficial effect of more fungal resources was counteracted by a lesser amount of grass litter in the vicinity of spruce boles.

Introduction

Forestry is becoming more intensive in northern Europe. In particular, harvesting of logging residue and stumps for fuel is rapidly increasing. Research on whole-tree harvesting has focussed on plant nutrients, and removal of logging residue has been considered good for the nutrient balance in areas suffering from high nitrogen deposition rates (Lundborg 1997).

Heterotrophic decomposers, however, are limited by carbon especially during the first year after clear-cutting. For example, clear-cutting temporarily reduces microbial biomass and respiration (Siira-Pietikäinen *et al*. 2001) and nematode abundance (Sohlenius 1982) even if logging residue is left on the site. Humans and decomposers are competing for energy. Given the short generation time of soil organisms, the period before ground vegetation appears in a clear-cut area may be extensive enough to affect their population dynamics.

Enchytraeids are keystone organisms in boreal coniferous forest ecosystems. Their biomass (about 10 kg fresh weight (FW) ha^{-1}; eg. Huhta and Koskenniemi 1975) may exceed moose biomass (< 5 kg FW ha^{-1}) in a typical Finnish forest. The dominant enchytraeid species in northern coniferous forests is *Cognettia sphagnetorum*, which normally reproduces asexually. Asexual reproduction has been considered more economical than sexual reproduction in poor habitats (Standen 1973), but more risky in changing environments (Lynch 1984).

Tree boles themselves are unavailable for enchytraeid consumption for decades; the decom-

position rate of conifer boles is usually less than 2% per year (Fahey 1983, Hyvönen *et al*. 2000). Because the nitrogen content of wood is low compared with fungal demand, hyphal growth for nutrient translocation in the surrounding soil can be expected. Fahey (1983 and references therein) provided empirical support for nitrogen translocation from soil to boles by comparing the N concentration dynamics of boles with or without contact with the forest floor. Using a field bating technique, Springett and Latter (1977) showed that enchytraeids colonized agar disks containing fungi, but not control disks. Thus, I hypothesized that fungal outgrowth from boles attracts enchytraeids in the long term. Enchytraeids may, however, benefit from the boles also because they provide physical cover and moisture reserves during periods of drought.

The effects of spruce boles on enchytraeid populations were investigated at plot scale and on a small scale (< 10 cm from boles). I also explored whether the size distribution of enchytraeids in the experimental plots differed from that in an uncut spruce forest.

Theory

Let r be the N/C ratio of fungal biomass, e fungal production to consumption ratio (efficiency), c_w wood carbon concentration, V bole volume, r_w wood N/C ratio, and N_s soil N concentration. Because the wood N/C ratio is lower than the critical N/C ratio r_c (Ågren and Bosatta 1996: 25; Table 1)

$$r_c = er = 0.006 > r_w, \qquad (1)$$

the boles will immobilize N from soil. To calculate how far from the bole nitrogen is immobilized, assume a cylindrical bole with a radius R and height h. Then the difference between the nitrogen supply (N in the bole) and fungal nitrogen demand (assuming the all C of the wood is eventually utilized) is (cf. eq. 3.3 in Ågren and Bosatta 1996)

$$d = rec_w V - r_w c_w V = (re - r_w)c_w V \qquad (2)$$

We get the area of forest floor containing this amount of nitrogen by dividing d by N_s. In particular, we can calculate when the projected area of the bole (right-hand side in Eq. 3) is insufficient to provide the nitrogen needed to decompose the bole:

$$\frac{1}{N_s}\left(re - r_w\right)c_w \pi R^2 h > 2Rh\ , \qquad (3)$$

from which R can be solved:

$$R > \frac{2N_s}{\pi\left(re - r_w\right)c_w}\ . \qquad (4)$$

Using very conservative parameter values (Table 1), the model gives $R = 0.07$ mm (kg N ha)$^{-1}$. Assuming that all nitrogen in the organic layer is available for decomposer fungi (which is not true), we get, using an average soil N content for Finnish spruce forests (Mälkönen 1977) 500 kg N ha^{-1}, an upper limit radius of 35 mm. This means that all boles with $R > 35$ mm (and possibly even smaller) immobilize N from the surrounding soil.

Material and methods

The study site was an 80-year-old Norway spruce (*Picea abies*) stand (ca. 8 ha, total wood volume ca. 2000 m^3) in western Finland, 40 km NE of

Table 1. Parameters of the model used to predict fungal N immobilization from soil surrounding decomposing Norway spruce boles.

Parameter	Symbol	Unit	Value	Source/notes
Fungal N/C ratio	r	–	0.05	C/N = 8 in Lavelle and Spain (2001). Most biomass is assumed to be hyphal walls with lower N content.
Fungal efficiency	e	–	0.125	Ågren and Bosatta (1998): 0.25. A lower value was used for a conservative estimate.
Wood C content	c_w	kg m^{-3}	169.5	Mälkönen (1977): spruce wood 339 kg m^{-3}, 50% C.
Wood N/C ratio	r_w	–	9×10^{-4}	Mälkönen (1977): spruce wood 339 kg m^{-3}, 153 g N m^{-3}.

Tampere (61°42´N, 24°05´E), between 145 and 160 meters above sea level). The stand was thinned in 1970. The southern end of the clear-cut area was a mossy *Myrtillus*-type site with thick organic layer, and the northern part was an *Oxalis–Myrtillus*-type site (Cajander 1926) with a thinner and drier humus layer, and herbs and grasses in the field layer. The pH (H_2O) of the soil was 4.66 ± 0.23 (mean ± SD).

The stand was clear-felled in June 2001, harrowed in August, and planted with 2-year old Norway spruce seedlings (1–9 tree seedlings per plot) after snow melt in early May 2002 according to normal practice (Metsätalouden kehittämiskeskus Tapio 2001). Eighteen 16 m^2 plots were then marked along the principal axis (SE–NW) of the area. The minimum distance between seedlings was 2 m; no samples were taken from the tree rhizosphere during the experiment. The experiment began in May 2002 when spruce boles were returned to every second plot. Given the size and shape of the area, the number of preselected plots, and the research facilities, a systematic scheme was considered better than randomization to ensure even distribution of plots over the area and to avoid edge effects. Each plot received 104 ± 111 dm^3 wood (mean ± SD, including bark), range 25–350 dm^3. Number of boles varied from three to eight. The diameter of the largest bole varied between 10.5 and 45 cm. The volume of the largest bole correlated significantly with the total wood volume per plot (Pearson correlation $r = 0.993$, $p < 0.001$). The amount of wood reflected initial variation at the site, because the boles belonging to a specific plot were brought back to the same plot after harvest, and no extra wood was added.

Enchytraeid soil cores (57 mm diam., 3 cm deep) were sampled at the experimental plots in October 2002, one growing season after the wood addition treatment. One sample per plot was taken beside the largest bole in the plot. Samples from control plots were taken close to the marked centre of the plot. Samples were transported in a cooler to the laboratory and were stored at +5 °C until extraction. Extraction was completed within five days from sampling. Enchytraeids were extracted using the Baermann wet funnel technique (O'Connor 1957) for 4 h. Subsamples of soil were weighed, oven-dried (+65 °C) for 24 hours, cooled in a desiccator and weighed again, and moisture percentage was calculated as a difference. Animal abundances were reported per dry mass (d.m.).

The main sampling was carried out in May 2007. Enchytraeid samples were taken as described above. Two adjacent enchytraeid samples were taken from the wood plots, one beside the bole (distance from bole 0–6 cm), and another at a 7–13 cm distance from the bole. Additional samples were taken from an adjacent uncut forest ("forest samples", $N = 5$). Living worms were counted immediately after extraction. For size determinations, test tubes containing enchytraeids were kept in hot water until the animals did not move. The lengths of worms were then measured using a stereomicroscope. All intact individuals of a sample were measured (min. 15 individuals per sample). The number of measured individuals varied, because damaged or irregular worms were not measured. A circular sample of ground vegetation (8.1 dm^2) was taken from each plot in July 2007, when the vegetation biomass had reached its annual maximum. Vegetation samples were taken beside the same boles as enchytraeid samples, but excluding the holes created by the soil corer. The vegetation samples were oven-dried at 65 °C, cooled in a desiccator and weighed.

The effect of wood addition on enchytraeid population density one and five years after the clear-cutting was tested with ANOVA for a repeated measurements design. The effect of distance from bole in 2007 was tested using Student's paired samples *t*-test (< 6 cm compared with 7–13 cm), and the effect of boles on the biomass of ground vegetation was tested using Student's *t*-test. Population densities (x) were normalized using a logarithmic transformation $\ln(x + 1)$. The length distributions of individual worms in control plots, wood plots and in forest samples were compared using one-way ANOVA and LSD was used to detect pairwise differences. The statistical analyses were carried out with SPSS® for Windows 14.0.

Results

Enchytraeid population densities ranged from 0

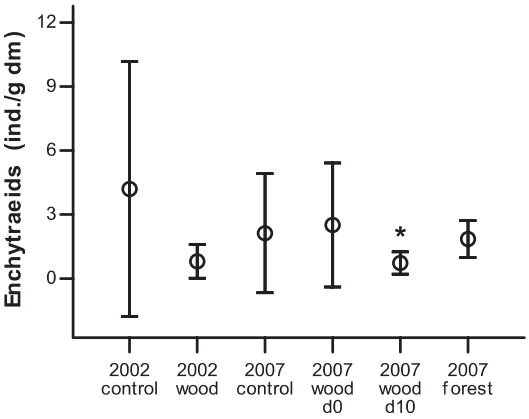

Fig. 1. Mean enchytraeid abundance (± SD) in control plots (without logging residues), wood plots (with spruce boles) and forest plots (nearby spruce forest) in October 2002 and May 2007. D0 = 0–6 cm distance from bole, d10 = 7–12 cm distance from bole. Data from the forest were not included in ANOVA. Effect of distance from bole was tested separately (**t*-test: $p = 0.036$).

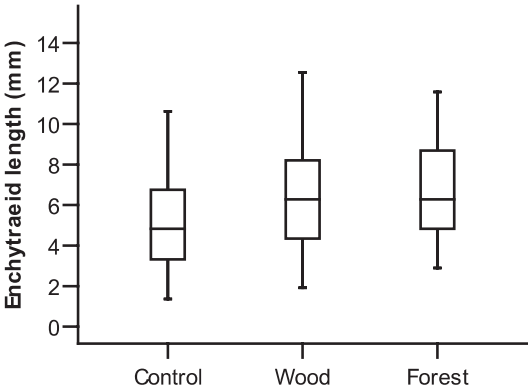

Fig. 2. Boxplots (median and interquartile ranges) for enchytraeid length (mm) distribution (pooled data) in control plots (without logging residues, $N = 207$), wood plots (with spruce boles, $N = 219$) and forest plots (nearby spruce forest, $N = 39$). Pairwise comparisons: LSD, Control–Wood $p = 0.01$, Control–Forest $p = 0.118$, Wood–Forest $p = 0.995$.

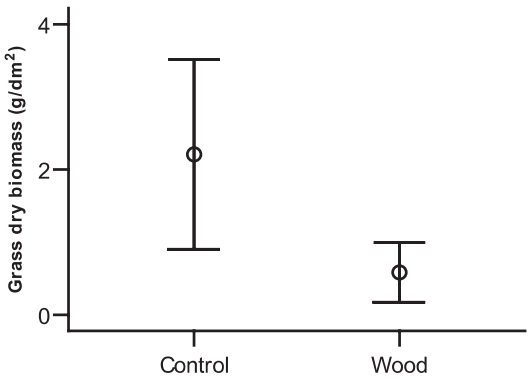

Fig. 3. Grass biomass (mean g dry mass dm^{-2} ± SD) in control plots (without logging residues) and wood plots (with spruce boles), $p < 0.05$ (*t*-test).

to 116 000 ind. m^{-2} (20 967 ± 27 458, mean ± SD, $N = 43$) in the experimental plots and from 4400 to 42 400 ind. m^{-2} (26 720 ± 14 061, mean ± SD, $N = 5$) in a nearby spruce forest. Wood addition had no significant effect on enchytraeid abundance (Fig. 1; ANOVA: Time $F_{1,14} = 0.164$, $p = 0.67$, Wood $F_{1,14} = 0.347$, $p = 0.3$, Time × Wood $F_{1,14} = 1.377$, $p = 0.23$). The variation of enchytraeid abundance was highest in control plots in 2002 (SD = 6 compared with < 3 in other treatment combinations) due to extreme densities in two plots. However, in the wood plots in 2007 there were significantly more enchytraeids close to the bole than at 7–13 cm distance from the bole (Fig 1., paired samples *t*-test, $t_8 = 2.5$, $p = 0.036$).

In 2007, the enchytraeids were shorter in the control plots than in the wood plots (Fig. 2, one-way ANOVA: $F_{2,384} = 3.636$, $p = 0.027$). Distance from bole had no significant effect on worm length (*t*-test assuming equal variances $t_{169} = 0.715$, $p = 0.476$).

The biomass of grasses and herbs was 3.8 times higher in the control plots than beside spruce boles in wood plots (Fig. 3; *t*-test assuming unequal variances, $t_{10} = 3.56$, $p = 0.003$).

Enchytraeid population densities were not significantly correlated with soil moisture percentage in 2007 ($r = –0.227$, $p = 0.12$, $N = 48$). The wood treatment did not affect soil moisture (ANOVA: Time $F_{1,14} = 0.015$, $p = 0.368$, Wood $F_{1,14} = 0.008$, $p = 0.514$, Time × Wood $F_{1,14} = 0.004$, $p = 0.629$). Enchytraeid densities were not spatially autocorrelated between consecutive plots ($r_1 = 0.022$, $p = 0.93$, $N = 17$), nor between control and treatment plots ($r = 0.423$, $p = 0.257$, $N = 9$).

Discussion

The population densities of enchytraeids observed in the present study are comparable to

those reported by Siira-Pietikäinen *et al*. (2001) during the first year after felling regardless of felling intensity. In their study, enchytraeid numbers started to increase in the second year after felling and they were highest in clear-felled plots. No increase of enchytraeid population was detected in the present study, because there were no samplings between 2002 and 2007. Huhta *et al*. (1986) reviewed that enchytraeid densities generally range from 27 500 to 40 000 ind. m^{-2}, but densities up to 90 000 ind. m^{-2} are recorded occasionally.

I hypothesized that the effect of boles on enchytraeids be positive because of fungal outgrowth and physical cover, but the effects turned out to be more complex. Enchytraeid population density in the immediate vicinity of the boles did not differ from that in the control plots. Although wood addition did not significantly affect enchytraeid abundance, the worms were significantly larger in wood plots than in control plots. If fragmentation is an adaptation to escape unfavourable conditions (Standen 1973, Haimi *et al*. 2006), this may mean that the wood plots were more favourable, or that the worms fragmented later in the wood plots than in the control plots. Enchytraeids suffered from the exceptionally warm and dry summer 2006 in Finland, and were scarce in samples taken in the autumn (J. Haimi pers. comm.), but the following short, warm and wet winter enabled fast recovery of decomposer populations by the sampling in May. On the basis of long-term time series, *C. sphagnetorum* is known to recover quickly from drought (Huhta 1969, Römbke 1991). Nevertheless, the drought may have been more severe in control plots and this may have been reflected in the size distribution observed in the following spring.

Enchytraeid densities and biomasses were higher at 0–6 cm distance than at 7–13 distance from the bole (Fig. 1), and grass biomass was significantly lower beside boles than in control plots (Fig. 3). Given that distance from bole did not affect worm size, it follows that enchytraeid biomass varied similarly as population density, and hence it is not necessary for the purposes of the present discussion to convert densities into biomasses. If the population density had been higher beside the boles, it could have been explained by movement of worms towards the boles. However, no crowding close to the boles was detected, suggesting that the overall effect of wood on enchytraeids was negative and that this was partially counteracted by a smaller positive effect at 0–6 cm from the boles.

Enchytraeid population density typically increases after clear-cutting (Huhta 1976, Lundkvist 1983, Siira-Pietikäinen *et al*. 2001). Whole-tree harvesting has been shown to have a positive short-term (2.5 yr) effect on enchytraeid abundance (Lundkvist 1983) but no long-term (15–18 yr) effect (Bengtsson *et al*. 1997). Another explanation of the increase of enchytraeids after clear-cutting even when logging residue is harvested, is that they benefit from eutrophication of field layer vegetation and a higher water table. Nitrophilous grasses such as *Deschampsia* spp. may produce both root exudates (Grayston *et al*. 1996) and relatively high quality litter. Because clear-cut areas of fertile sites are rich in light and nitrogen, they are often initially dominated by a few grass species, which do not have to invest much for competition with other plants. In an experiment by Makulec and Pilipiuk (2000) there indeed were fewer enchytraeids in field lysimeters with a combination of six grass species than in pots with a single grass species.

If boles are left on clear-cut areas, wood decomposing fungi can be expected to compete with grasses for nitrogen. If grass litter is a better resource for enchytraeids than wood decomposing fungi, a reduction in grass biomass would be reflected in a reduction in enchytraeid population. Therefore competition between fungi and grasses can be considered a likely explanation of the negative effect of wood on enchytraeids.

Because in the experiment $\min\{\max\{R\}\}$ = 50 mm, where the maximum is taken within and the minimum taken between plots, the model (Eq. 4) predicts N immobilization from the soil surrounding the bole in each experimental plot. Thus it can be concluded that the explanation based on N immobilization and competition between wood-decomposing fungi and grasses is quantitatively plausible.

Woody debris has been shown to suppress the growth of graminoids, but only eight years after clear-cutting (Olsson and Staaf 1995). However, Olsson and Staaf (1995) estimated

the grass cover by naked eye, and the scale was also quite large (2.9 m^2) from the enchytraeid viewpoint. The negative effect of wood on the biomass of ground vegetation was more apparent in the present study probably because the plots were smaller and the vegetation samples were taken close to the boles (Fig. 3). The negative effects of logging residues on ground vegetation, and subsequently to decomposers, are transient because eventually the immobilized nutrients are released. Bråkenhielm and Liu (1998) found that logging residue increased grass biomass 20 yr after clear-cutting.

Provided that fungi need to immobilize nutrients from surrounding soil so as to decompose wood, fungal-feeding animals may hypothetically retard wood decomposition by eating the fungal hyphae, but this remains to be experimentally verified in the field. Positive and negative effects of soil fauna on decomposition have indeed been observed in small-scale experiments with a variety of substrates (Huhta *et al*. 1998). An immobilization phase may be needed before conifer needles commonly used in such experiments (N/C ratio about 0.02) can be decomposed by fungi ($N/C \approx 0.05$). For example, lodgepole pine (*Pinus contorta* ssp. *latifolia*) needles immobilized nitrogen for two years in a field study (Fahey 1983).

Fahey (1983) estimated that pine boles immobilized 0.12 g N m^{-2} yr^{-1} and this was suggested to be due to translocation from the forest floor by filamentous fungi. Olsson *et al*. (1996) showed that N loss from the humus layer was greatest in a conventionally harvested (residue left on site) spruce forest. Since that forest was the most productive site in their study, also the amount of logging residue C was large (over two times the amount in the least fertile site) (Olsson *et al*. 1996). It is possible that the immobilization in logging residue was also highest there. More recently, studies have found that logging residues have reduced mineral nitrogen in soil (Perez-Batallon *et al*. 2001, O'Connell *et al*. 2004) and increased microbial biomass carbon (Perez-Batallon *et al*. 2001, Mendham *et al*. 2002) in various ecosystems, but to my knowledge, the feedback residue–fungi–vegetation–enchytraeids–fungi has gone largely unnoticed.

Eventually, even the largest boles will be exhausted as a C source, and the nutrients will become available to plants again. Clear-cut areas, in which grasses thrive in the field layer (Olsson and Staaf 1995) and bacteria dominate the microbial community (Siira-Pietikäinen *et al*. 2001) resemble more an agricultural system than a mature forest, and consequently grass rhizosphere may be more important for decomposers than wood. It can be anticipated that the interaction of large boles and decomposer animals be different in natural forests, in which shadowing by trees controls grass growth, and it would be interesting to compare intensively managed and natural forests from this point of view. The natural condition has just become rare — fallen trees are normally removed from commercial forests.

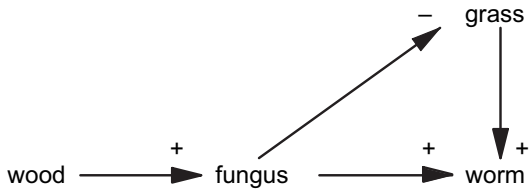

Fig. 4. Decomposing wood is a resource for fungi, fungal biomass and grass litter are resources for enchytraeid worms. The positive effect of wood on enchytraeids may be offset by a negative effect of fungal competition for N on grass production. In addition, wood may have nontrophic (physical) effects on decomposers (not shown).

Conclusion

Spruce boles had no statistically significant effect on enchytraeids as compared to control plots without wood. However, the enchytraeid density significantly decreased within a 10 cm distance from the boles. Opposite effects of logging residue on soil animals may cancel each other when scaled up to the plot level (Fig. 4). Wood is not only a basal resource for the fungal-based food chain, but it also affects the competition for nutrients between fungi and ground vegetation. Thus plot-scale experiments may miss some effects of logging residue on soil fauna because of trophic-dynamic as well as statistical reasons. Smaller-scale models and experiments are needed to fully understand the effects of logging residue on the decomposer food web.

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